

FAUNAL SUCCESSION AND MODE OF LIFE OF SILURIAN GASTROPODS IN THE ARISAIG GROUP, NOVA SCOTIA

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ABSTRACT. Three basic types of Silurian gastropod faunas are recognized in the near-shore deposited Arisaig Group, Nova Scotia. A hard-bottom, shallow marine platform fauna is characterized by trochiform pleurotomariaceans. A soft-bottom, shallow marine platform fauna has dominant high-spined gastropods, and lacks the trochiform pleurotomariaceans. A more off shore, soft-bottom, open-lagoon fauna is typically composed of trochiform holopeids, although these give way to small bellerophontaceans in shallower water. Morphologically similar, but taxonomically different, faunas reoccur with repetition of environments in successive regressive sedimentary phases.

High-spined gastropods and explanate bellerophontaceans show morphological adaptations to life on a soft bottom. Trochiform pleurotomariaceans were associated with a harder bottom, while many other Arisaig gastropods were probably algal foliage dwellers.

SILURIAN gastropods from the near-shore deposits of the Arisaig Group, Nova Scotia (text-fig. 1) followed a number of modes of life reflecting differences in the environments in which they lived. The modes of life are to a large extent inferred from interpretations of shell functional morphology. However, the nature of the enclosing sediment and the gross size of individual gastropods provide additional discriminating characters which are particularly important to the evaluation of algal-foliage supported modes of life.

Three basic gastropod faunas within the Arisaig Group are related to specific bottom conditions and distance from shore. Each faunal grouping is characterized by distinct gastropod morphotypes. The faunas are repeated in successive regressive phases during the depositional history of the sequence, although few species persist from one regressive phase to the next. The re-establishment of morphologically similar, but taxonomically dissimilar, gastropod faunas with the repetition of comparable sedimentary environments suggests strong correlation between shell form in Arisaig gastropods and the physical environment.

THE GASTROPOD FAUNA

Gastropods were first described from the Arisaig Group by Hall (1860) who named two characteristic high-spined murchisoniids, *Murchisonia (M.) aciculata* and *M. (?Hormotoma) arisaigensis*, and the still unique specimen of *Onychochilus(?) reversa*. Dawson (in Honeyman 1860) supplied notes on several common species but without illustration. The general faunal monograph of McLearn (1924) included eighteen species of gastropods, of which six species and one variety were new. A recent series of papers by Peel (1974; 1975a-c; 1977) has increased this total to more than sixty species and provides the taxonomic base for the present paper (text-fig. 2).

The trilobed bellerophontaceans *Plectonotus* and *Tritonophon* (Pl. 27, figs. 3, 8, 20) are represented by five species distributed throughout the sequence (text-fig. 2).



TEXT-FIG. 1. The Arisaig region, Nova Scotia. Ac, Antigonish County; Pc, Pictou County; Fr, French River; Su, Sutherland River.

Trochiform pleurotomariaceans (Pl. 27, figs. 15, 18, 22) dominate the Beechhill Cove Formation (*Loxoplocus*, *Arjamannia*, *Longstaffia*, *Phanerotrema*) but also occur rarely in other formations. The trochiform holopeids *Holopea* and *Gyronema* (Pl. 27, figs. 1, 4) are abundant in the Ross Brook Formation and the former reappears in the McAdam Brook Formation. High-spired murchisoniids (Pl. 27, figs. 14, 19) and loxonemataceans (Pl. 27, figs. 11, 16) are frequently abundant and dominate in the lower Moydart and upper Stonehouse formations. Other characteristic elements include trochiform platyceratids (Pl. 27, figs. 2, 23), explanate bellerophontaceans (Pl. 27, fig. 5), lenticular pleurotomariaceans (Pl. 27, figs. 7, 9, 13), a trochiform murchisoniacean (Pl. 27, fig. 10), and several small bellerophontaceans (Pl. 27, figs. 12, 17, 21).

This gastropod fauna shows great similarity to contemporaneous faunas from level-bottom communities in the Silurian of Britain described by Sowerby (*in* Murchison 1839), Longstaff (1924), Straw (1933), and Pitcher (1939). Gastropod faunas from Silurian carbonate sequences in Europe (Lindström 1884) and North America (Hall 1852; Whiteaves 1895; Northrop 1939; Poulsen 1974) are not similar taxonomically.

TEXT-FIG. 2. Distribution of gastropods within the Arisaig Group. Numbers to the left of species names refer to the morphological groupings employed in the text. 1, high spired. 2, micromorphic high spired. 3, explanate bellerophontacean. 4, micromorphic bellerophontacean. 5, trilobed bellerophontacean. 6, other small bellerophontaceans. 7, lenticular pleurotomariacean. 8, trochiform pleurotomariacean. 9, trochiform murchisoniacean. 10, trochiform platyceratid. 11, trochiform holopeid. 12, other gastropods.

6	undet. bellerophontacean sp. A	_____								5	Plectonotus cherylae	_____
6	undet. bellerophontacean sp. B	_____								5	Tritonophon kivitalonae	_____
7	Liospira cf. L. affinis	_____								3	Anapetopsis maclearni	_____
8	Loxoplocus (Lophospira) sedgwicki	_____								3	A. lalajae	_____
8	L. (Lo.) sp. A	_____								6	undet. bellerophontacean sp. D	_____
8	L. (Lo.) sp. B	_____								12	Onychochilus (?) reversa	_____
8	Longstaffia sp.	_____								7	Liospira marklandensis	_____
8	Arjamannia cancellatula	_____								8	Brachytomaria sp.	_____
8	A. woodlandi	_____								12	Platyconus (?) sp.	_____
8	Phanerotrema affin. P. jugosum	_____								12	undet. trochonematid sp.	_____
10	Naticonema kauffmani	_____								12	Haplospira sibeluxeni	_____
10	Cyclonema (C.) parvimedium	_____								10	Cyclonema (C.) lydiamarium	_____
12	undet. trochinid sp.	_____								1	Murchisonia (M.) aciculata	_____
7	Eotomaria sp.	_____	_____							1	M. (M.) amii	_____
8	Longstaffia centervillensis	_____	_____							1	M. (?Homotoma) arisaigensis	_____
12	undet. holopeid sp.	_____	_____							1	Loxonema sinuosum	_____
10	Platyceras (P.) cf. Pl. (P.) humilis	_____	_____							1	Morania (?) boltoni	_____
7	Umbospira yochelsoni			_____						12	Auriptygma sp.	_____
11	Gyronema haliburtoni			_____								
1	Murchisonia (Homotoma) sp. A			_____								
1	Loxonema sp. B			_____								
5	Tritonophon sp.	_____		_____								
6	Bucanopsis sp.	_____		_____	_____							
11	Holopea rossbrookiensis			_____	_____							
6	undet. bellerophontacean sp. C				_____							
4	Tropidodiscus (?) arisaigensis					_____						
8	Arjamannia aulangenensis					_____						
6	Cymbularia sp.					_____						
5	Plectonotus boucoti					_____						
6	Pharetrolites bambachi						_____					
1	M. (Sinuspira) cf. M. (S.) tenera						_____					
2	Morania (?) sp.						_____					
1	Loxonema sp. A						_____					
1	Murchisonia (Homotoma) sp. B							_____				
12	Mimospira abbae							_____				
5	Tritonophon trilobata								_____			
3	Phragmosphaera globata									_____		
6	Cymbularia carinata										_____	
12	undet. gyronematid sp.											_____
12	Naticopsis trevorpatriciorum											_____
2	Murchisonia (s.l.) antigonishensis											_____
9	Seelya moydartensis											_____
6	Pharetrolites murchisoni											_____
10	Platyceras (P.) cornutum	_____										_____
	undet. high spired gastropods	_____	_____									_____
	undet. gastropods	_____	_____	_____								_____

BEECHHILL COVE FM.	L	M.	U.	FRENCH RIVER FM.	DOCTORS BROOK FM.	L	U.	L	U.	STONEHOUSE L.	U.
	ROSS	BROOK	FM.			McADAM	BROOK FM.	MOYDART	FM.		FM.
LLANDOVERY				WENLOCK		LUDLOW				PRIDOLI	

Consequently, such widely distributed and well-known Silurian gastropods as the strongly ornamented *Poleumita* and the flange-bearing *Euomphalopterus* have not been recorded from Arisaig, although they may also prove to be characteristic of more off-shore assemblages than those preserved in this area (Boucot 1975).

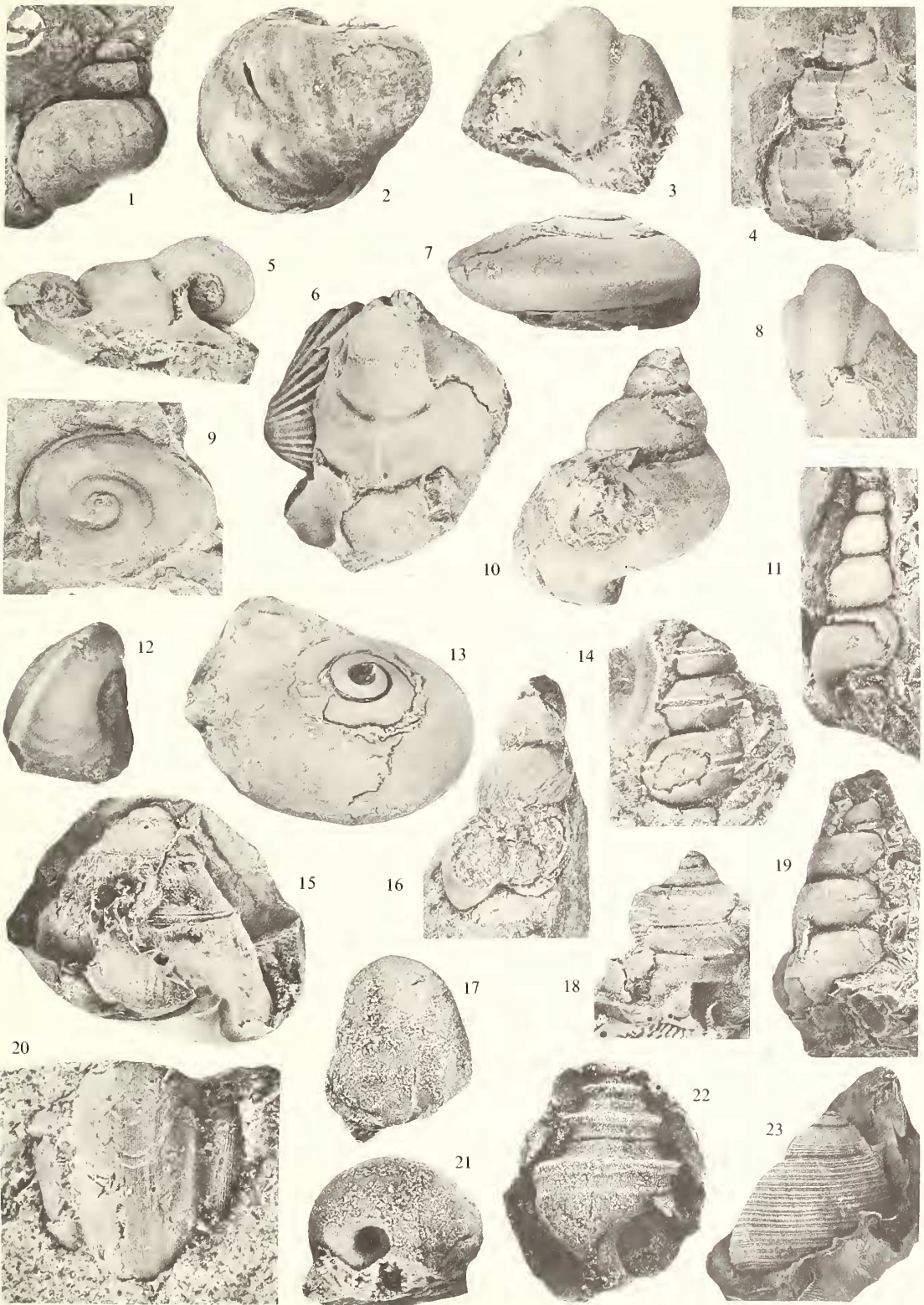
PALAEOENVIRONMENTS OF THE ARISAIG GROUP

Boucot *et al.* (1974) remarked that the Arisaig Group (text-figs. 2, 3) is unique in providing an almost continuous faunal record of a shallow marine environment

EXPLANATION OF PLATE 27

GSC = Geological Survey of Canada, Ottawa; USNM = U.S. National Museum, Washington D.C.; YPM = Yale Peabody Museum, New Haven.

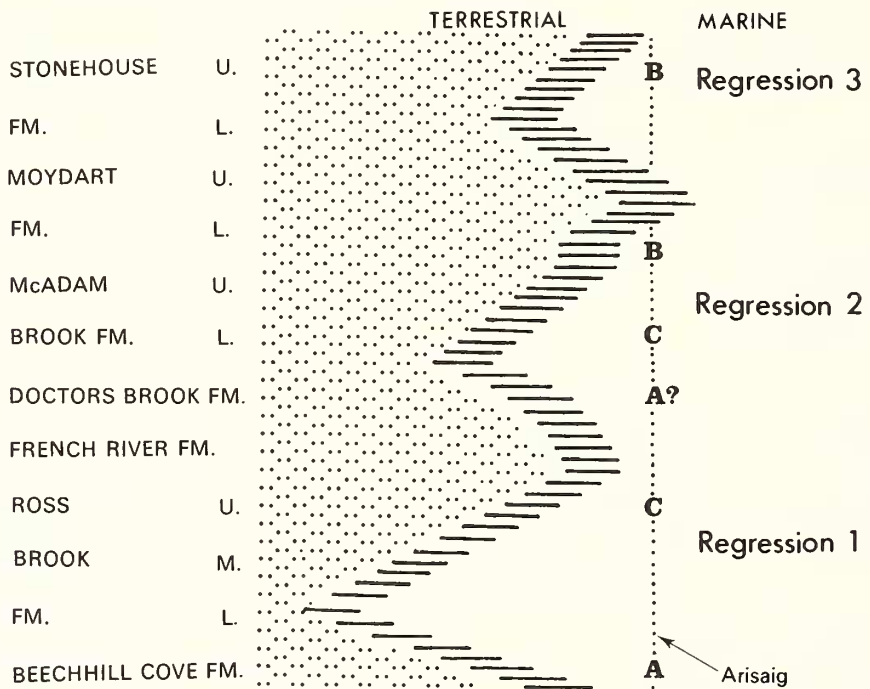
- Fig. 1. *Holopea rossbrookiensis* Peel, 1977. Trochiform holopeid, upper Ross Brook Fm. YPM 28333, holotype, $\times 2$.
- Fig. 2. *Platyceras (Platystoma) cornutum* (Hisinger, 1837). Coprophagous trochiform platyceratid, lower Moydart Fm. GSC 33272, $\times 2$.
- Fig. 3. *Tritonophon kivialtonae* Peel, 1974. Trilobed plectonotid bellerophontacean, upper Stonehouse Fm. GSC 32782, $\times 3$.
- Fig. 4. *Gyronema haliburtoni* (McLearn, 1924). Trochiform holopeid, upper Ross Brook Fm. YPM 462B, holotype, $\times 3$.
- Figs. 5, 6. *Anapetopsis maclearni* Peel, 1975a. Explanate bellerophontacean, upper Stonehouse Fm. GSC 3140a, holotype, $\times 2$.
- Figs. 7, 13. *Liospira marklandensis* McLearn, 1924. Lenticular pleurotomariacean, upper Stonehouse Fm. GSC 5654, holotype, $\times 2$.
- Fig. 8. *Tritonophon trilobata* (Sowerby in Murchison 1839). Trilobed plectonotid bellerophontacean, lower Moydart Fm. USNM 169594, $\times 3$.
- Fig. 9. *Umbospira yochelsoni* Peel, in press. Lenticular pleurotomariacean, upper Ross Brook Fm. YPM 28330, holotype, $\times 2$.
- Fig. 10. *Seelya moydartensis* McLearn, 1924. Trochiform murchisoniacean, lower Moydart Fm. YPM 464A, $\times 1$.
- Fig. 11. *Loxonema sinuosum* (Sowerby in Murchison 1839). High-spined loxonematacean, upper Stonehouse Fm. YPM 28337A, $\times 3$.
- Fig. 12. *Pharetrolites murchisoni* (d'Orbigny, 1848). 'Other' bellerophontacean, lower Moydart Fm. USNM 169461, $\times 2$.
- Fig. 14. *Murchisonia (M.) aciculata* Hall, 1860. High-spined murchisoniid, upper Stonehouse Fm. GSC 5651, $\times 4$.
- Fig. 15. *Arjamannia aulangonensis* Peel, 1975b. Trochiform pleurotomariacean, Doctors Brook Fm. USNM 169469, holotype, $\times 2$.
- Fig. 16. *Morania(?) boltoni* Peel, 1975c. High-spined loxonematacean, upper Stonehouse Fm. USNM 192120, holotype, $\times 2$.
- Figs. 17, 21. *Bucanopsis* sp. 'Other' bellerophontacean, Doctors Brook Fm. USNM 169466, $\times 2$.
- Fig. 18. *Longstaffia centervillensis* (Foerste, 1923). Trochiform pleurotomariacean, Beechhill Cove Fm. USNM 188524, $\times 2$.
- Fig. 19. *Murchisonia (M.) amii* (McLearn, 1924). High-spined murchisoniid, upper Stonehouse Fm. GSC 5652, holotype, $\times 3$.
- Fig. 20. *Plectonotus boucoti* Peel, 1974. Trilobed plectonotid bellerophontacean, Doctors Brook Fm. USNM 169583, $\times 5$.
- Fig. 22. *Loxoplocus (Lophospira)* sp. A. Trochiform pleurotomariacean, Beechhill Cove Fm. USNM 169482, $\times 2$.
- Fig. 23. *Cyclonema (C.) parvimedium* McLearn, 1924. Trochiform platyceratid, Beechhill Cove Fm. USNM 169473, $\times 1$.



PEEL, Silurian gastropods

throughout the Silurian. Watkins and Boucot (1975) subsequently discussed the succession of brachiopod communities at Arisaig and concluded that most could be referred to the near-shore Benthic Assemblage 2 of Boucot (1975), although the French River Formation has an off-shore Benthic Assemblage 3 or 4 association.

Bambach (1969) presented a sedimentary facies model for the Arisaig Group in the course of an exhaustive study of bivalve palaeoecology. He accepted the general near-shore origin suggested by Boucot *et al.* (1974; in prep. at that time), in which even the deepest part of the succession (represented by the lower Ross Brook Formation) was considered to lie within the *Eocoelia* community of Boucot's Benthic Assemblage 2.



TEXT-FIG. 3. Distribution of gastropod faunas in the three regressive phases of the Arisaig Group. A, hard-bottom, shallow marine platform fauna. B, soft-bottom, shallow marine platform fauna. C, soft-bottom, open lagoon fauna. The vertical broken line represents the approximate position of the Arisaig Group sequence in the simplified facies model (after Bambach 1969).

Bambach recognized three major regressive events during the deposition of the Arisaig Group (text-fig. 3). An initial transgression across underlying non-marine volcanics is represented by the Beechhill Cove Formation. Hard, grey-green quartzose siltstones and thin micaceous shales contain only linguloid brachiopods and crinoid ossicles, but occasional fine sandstone lenses, probably representing storm layers, contain brachiopod-rich basal coquinas.

The Ross Brook and French River formations represent a regressive phase with passage from the deepest water deposits of the Arisaig Group to shoaling barrier

deposits in the French River Formation. Fissile graptolitic shales in the lower Ross Brook Formation represent fine muds possibly with an originally high water content. Increased silt content in the middle and upper members of the Ross Brook Formation reflects shallowing and probably produced a stabilized substratum capable of supporting a rich epifauna. Massive siltstones with oolitic ironstone of the French River Formation were considered to represent a barrier bar behind which the shallow-water siltstones of the Doctors Brook Formation were deposited.

A second regressive phase followed an increase in water depth in the earliest McAdam Brook Formation where dark shales comparable to those of the lower Ross Brook Formation occur. Younger strata in the formation contain increasingly higher quantities of silt with massive shoreline siltstones characterizing the succeeding lower Moydart Formation. The regression continued with deposition of non-marine red beds in the upper Moydart Formation.

Massive shoreline siltstones again dominate the lower Stonehouse Formation, but are followed by open marine platform shales, siltstones, and thin limestones in the upper member. A third regression, producing a gradual shallowing in the later part of the upper Stonehouse Formation, culminates in a return to non-marine red bed deposition in the Devonian Knoydart Formation.

GASTROPOD FAUNAL TYPES

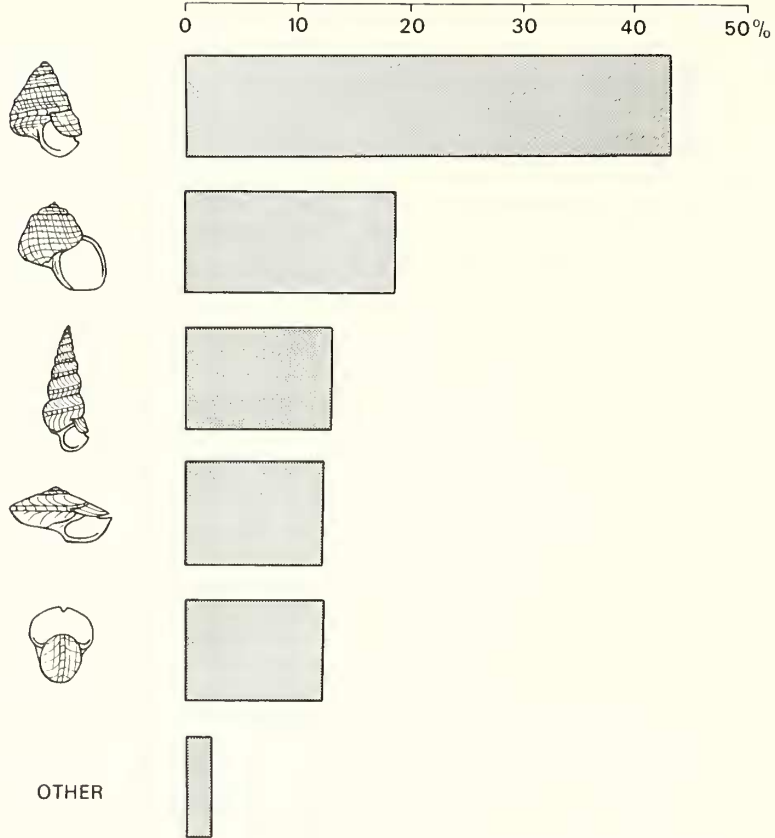
Three associations of gastropods are recognized in the Arisaig Group on the basis of their principal constituent morphological groups and partial recurrence in the sedimentary model of Bambach (1969). Interpretation of modes of life of gastropods within the morphological groups, which add further support to the delimitation of faunal types, is attempted in a later section.

Hard-bottom, shallow marine platform fauna. This fauna is characterized by a dominance of large (up to 25 mm) trochiform pleurotomariaceans, both in terms of individuals and number of species. Trochiform holopeids, explanate bellerophontaceans, and trochiform murchisoniaceans, interpreted below as associated with a soft bottom, are absent. High-spired gastropods are present, but not dominant as in the soft-bottom, shallow marine platform fauna.

The fauna is typically developed in the transgressive Beechhill Cove Formation (text-figs. 2, 4) where the large (20–30 mm) trochiform platyceratacean *Cyclonema* (*C.*) *parvimum* is also conspicuous. Lenticular pleurotomariaceans and the globose bellerophontacean *Bucanopsis* sp. (Pl. 27, figs. 17, 21) are also well represented, but not considered diagnostic.

The hard-bottom, shallow marine platform fauna may also be represented in the Doctors Brook Formation (text-figs. 2, 3), although trochiform pleurotomariaceans are rare, and trilobed plectonotid bellerophontaceans are dominant. This may suggest more shallow-water or near-shore conditions than in the Beechhill Cove Formation, where only a single plectonotid is recorded (see discussion below).

Soft-bottom, shallow marine platform fauna. The soft-bottom, shallow marine platform fauna is dominated by high-spired murchisoniids and loxonemataceans, associated

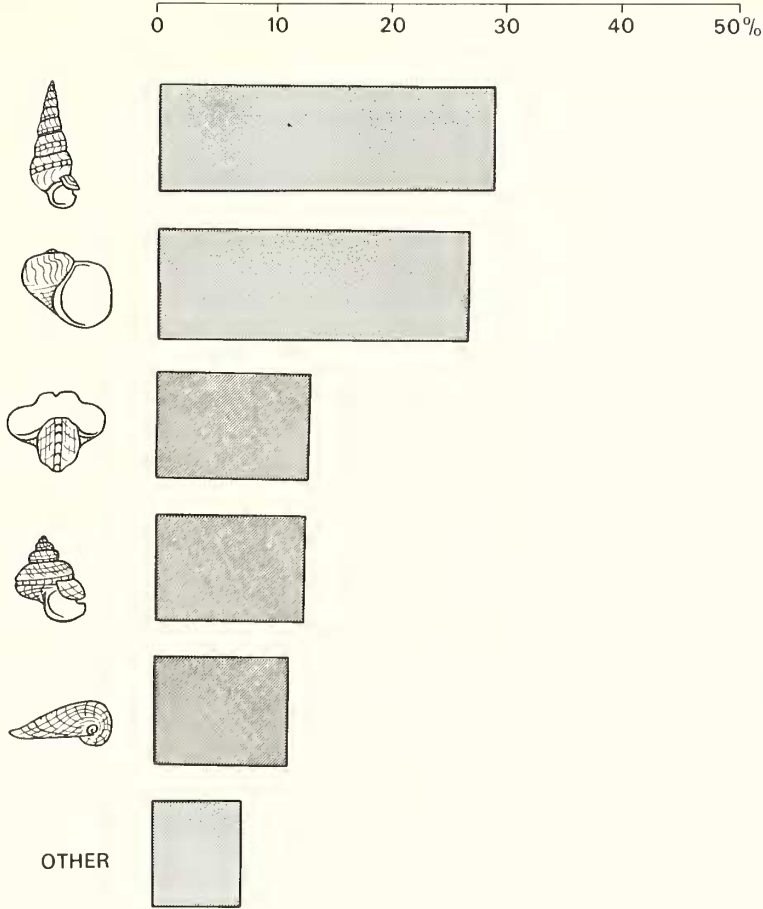


TEXT-FIG. 4. Composition of hard-bottom, shallow marine platform fauna, Beechhill Cove Formation. In descending order: trochiform pleurotomariaceans, the trochiform platyceratid *Cyclonema (C.) parvimedium*, high-spired gastropods, lenticular pleurotomariaceans, the small bellerophontacean *Bucanopsis sp.*, other gastropods. Total of 146 specimens.

with explanate bellerophontaceans and trochiform murchisoniaceans. Trochiform pleurotomariaceans are almost totally absent, in agreement with the interpreted soft bottom.

Trilobed plectonotid bellerophontaceans are common, but this abundance is primarily equated with proximity to shore rather than the nature of the sea bottom. Trilobed bellerophontaceans are also well represented in the possible near-shore equivalent of the hard-bottom, shallow marine platform fauna preserved in the Doctors Brook Formation, above, and in the soft-bottom open lagoon fauna described below.

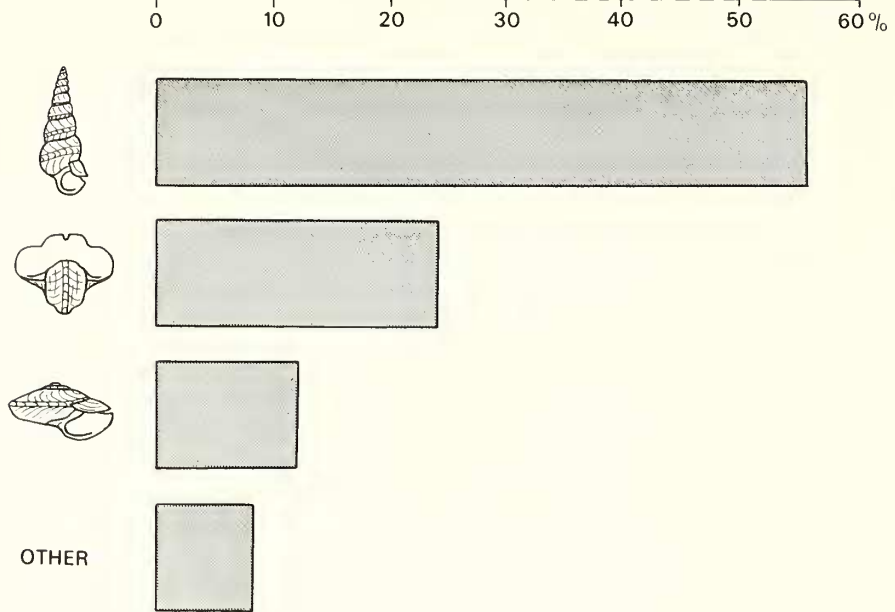
The soft-bottom, shallow marine platform fauna is well represented in the upper Stonehouse Formation and, in a more diverse form, in the lower Moydart Formation (text-figs. 2, 5, 6), the latter during a brief lull in massive shore-line siltstone deposition. In the Stonehouse Formation the lenticular pleurotomariacean *Liospira marklandensis*



TEXT-FIG. 5. Composition of soft-bottom, shallow marine platform fauna, lower Moydart Formation. In descending order: high-spired gastropods, the trochiform platyceratid *Platyceras (Platyostoma) cornutum*, trilobed bellerophontacean *Tritonophon trilobata*, trochiform murchisoniacean *Seelya moydartensis*, explanate bellerophontacean *Phragmosphaera globata*, other gastropods. Total of 159 specimens.

(Pl. 27, figs. 7, 13) is common, and the explanate bellerophontacean *Anapetopsis* (Pl. 27, figs. 5, 6) somewhat infrequent. In the Moydart Formation, the trochiform murchisoniaceans *Seelya moydartensis* and explanate bellerophontacean *Phragmosphaera globata* are common additional elements. Abundant coprophagous platyceratids reflect the presence of the best preserved crinoid remains in the Arisaig Group, but are not considered definitive of fauna B.

Soft-bottom, open-lagoon fauna. In its typical development in the lower beds of the upper Ross Brook Formation, this fauna is heavily dominated by the trochiform holopeids *Gyronema* and *Holopea* (Pl. 27, figs. 1, 4). With a decrease in water depth the holopeids are replaced by a fauna of small bellerophontaceans, including trilobed plectonotids,



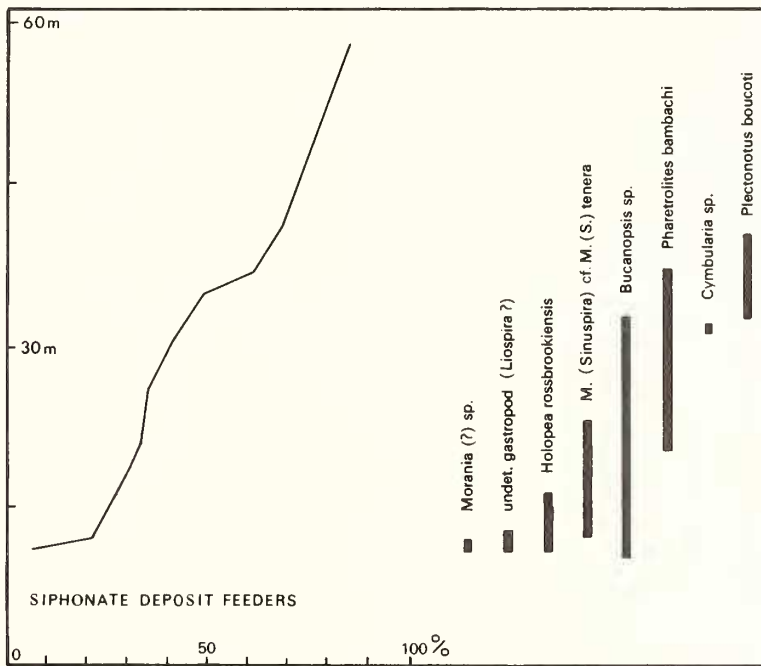
TEXT-FIG. 6. Composition of soft-bottom, shallow marine platform fauna, upper Stonehouse Formation. In descending order: high-spired gastropods, trilobed bellerophonaceans, the lenticular pleuromariacean *Liospira marklandensis*, other gastropods. Total of 353 specimens.

associated with lenticular pleuromariaceans and some high-spired gastropods. This shallower-water equivalent of the typical soft-bottom, open-lagoon fauna also lacks the abundant trochiform pleuromariaceans characteristic of the hard-bottom, shallow marine platform fauna, or the over-all dominance by high-spired gastropods typical of the soft-bottom, shallow marine platform fauna.

The soft-bottom, open-lagoon fauna is also preserved in the lower McAdam Brook Formation, although the typical holopeids are more restricted and soon give way to the more shallow-water elements. Here, a parallel change has been documented by Levinton and Bambach (1975) in the composition of bivalve faunas. Deposit feeding bivalves dominate throughout, but non-siphonate forms are gradually replaced by siphonate species in a change which Levinton and Bambach related to increasing firmness of the later, more near-shore deposits (text-fig. 7).

Comparable faunas from other areas. The parallel development of gastropod faunas respectively dominated by trochiform pleuromariaceans and high-spired gastropods, i.e. the hard-bottom, and soft-bottom, shallow marine platform faunas as reported above, has been described by Bretsky (1970) from the upper Ordovician of the central Appalachians. Lophospirid, trochiform pleuromariaceans occur in a *Sowerbyella-Omiella* Community developed on outer sublittoral sands, while high-spired murchisoniids are the characteristic gastropods in an inner to outer sublittoral *Zygospira-Hebertella* Community developed on calcareous muds.

An antipathetic relationship between trilobed plectonotid bellerophontaceans and the trochiform holopeid '*Gyronema cf. octavia*' described by Shaw (1971) from the upper Silurian of the English Lake District may represent the passage from a soft-bottom, open-lagoon fauna as interpreted here, to its near-shore equivalent with small bellerophontaceans. Shaw maintained that the holopeid dominated in more stable areas of slow sedimentation, while the plectonotid was typical of more rapidly sedimented, perhaps deeper-water areas. Shaw's conclusions with regard to depth are in apparent contradiction with the evidence from Arisaig, where plectonotinids are attributed a more near-shore life habit than trochiform holopeids. However, the presence of holopeids in the fine-grained sediments of the Ross Brook Formation may be in agreement with Shaw's observation concerning slow sedimentation. Similarly, the presence of trilobed plectonotinids higher in the inferred shallowing sequence, interbedded with shoal-deposited siltstones, may equally explain Shaw's claim for more unstable conditions.



TEXT-FIG. 7. Distribution of siphonate deposit-feeding bivalves, and gastropods in the lower McAdam Brook Formation. Increase in siphonate deposit feeders ascribed to increasing firmness of progressively more near-shore deposits parallels a gradual change in the gastropod fauna from elements of the soft-bottom, open lagoon fauna to more shallow-water equivalents. Bivalve and section data compiled after Bambach (1969) and Levinton and Bambach (1975). Total of 54 gastropods.

GASTROPOD FAUNAL SUCCESSION

The three generalized gastropod faunas described above are partially repeated in the Arisaig Group (text-fig. 3) as a result of the repetition of environments in the three regressive phases described by Bambach (1969). The repetition, which is particularly evident in the case of the two soft-bottom associations, serves to emphasize the integrity of the faunal division based on morphological groups, since very few species survive from one regressive phase to the next (text-fig. 2). However, morphologically equivalent species can be recognized in successive phases, and the gross morphological composition of the respective faunas is largely unchanged.

The hard-bottom, shallow marine platform fauna is developed in the transgressive Beechhill Cove Formation (fauna A in text-fig. 3) and succeeded by a soft-bottom, open lagoon fauna during the first regressive phase (fauna C). The few gastropods known from the French River Formation are too meagre to evaluate, but the hard-bottom fauna possibly reoccurs in the Doctors Brook Formation with rare specimens of a different species of the trochiform pleurotomariacean *Arjamannia* than those known from the Beechhill Cove Formation (text-figs. 2, 3).

The soft-bottom, open lagoon fauna is again evident in the second regressive phase, with *Holopea rossbrookiensis* reappearing in the McAdam Brook Formation after its initial occurrence in the Ross Brook Formation. *Bucanopsis* sp. also reappears, but new species of trilobed plectonotids and high-spined gastropods are found. The reduced representation of holopeids in the second regressive phase may suggest somewhat more near-shore conditions initially, relative to the first regressive phase, which is in accordance with Bambach's (1969) proposal that the lower Ross Brook Formation contains the deepest-water deposits within the Arisaig Group.

Later in the second regressive phase, the soft-bottom, shallow marine platform fauna occurs in the lower Moydart Formation (fauna B in text-fig. 3) prior to non-marine red-bed deposition in the upper Moydart Formation.

Sufficiently off-shore conditions suitable for the establishment of the open-lagoon fauna were not developed in the third sedimentary cycle. The soft-bottom, shallow marine platform fauna is, however, well represented in the upper Stonehouse Formation (B in text-fig. 3) before red-bed deposition once more returned in the overlying Knoydart Formation (Devonian). *Pharetrolites munchisoni* and the ubiquitous *Platyceras* (*Platyostoma*) *cornutum* reappear in the upper Stonehouse Formation, after being present in the previous regressive phase, but the morphologically similar faunas do not otherwise have species in common.

MODE OF LIFE OF LOWER PALAEOZOIC GASTROPODS

All the Arisaig gastropods listed in text-fig. 2, with the exception of six species assigned to the caenogastropods *Loxonema*, *Morania*?, and *Auriptygma*, were placed within the Order Archaeogastropoda by Knight *et al.* (1960). Recent members of the order are herbivores, which are generally restricted to a harder bottom in conditions of clear water, since their bipectinate ctenidia cannot satisfactorily cope with fine, suspended sediment (Yonge 1947). In contrast, living members of the Caenogastropoda (= Mesogastropoda + Neogastropoda), which now comprise two-thirds of

the prosobranch gastropod fauna of recent seas, have a monopectinate ctenidium enabling free movement into environments characterized by soft sediment.

The rise to dominance of caenogastropods since the Lower Palaeozoic has possibly resulted in a parallel diminution in the range of habitats occupied by archaeogastropods. Recent archaeogastropods may therefore have a narrower environmental range than their Palaeozoic ancestors, due to competition with the increasingly abundant caenogastropods. Thus, Lower Palaeozoic archaeogastropods should not *automatically* be interpreted as herbivores limited to hard bottoms in clear water in similar fashion to most of their extant descendants.

Some non-herbivores are already known in the Lower Palaeozoic—many platyceratids lived on the calyx of echinoderms and ingested expelled faeces (Bowsher 1955). Related platyceratids may easily have been benthic scavengers. True carnivorous gastropods have not been certainly recognized, although it is quite possible that some Palaeozoic gastropods fed on sponges in similar fashion to some extant 'primitive' archaeogastropods of the family Fissurellidae (Morton 1967).

Similarly, other Palaeozoic gastropods may be common in fine sediments seemingly indicative of a soft bottom (Foerste 1923; Craig 1954; Wilson 1966; Bretsky 1970). In some cases, as for example in the fauna of small Carboniferous gastropods from Poland described by Gromczakiewicz-Lomnicka (1972), the occurrence of gastropods can be satisfactorily interpreted in relation to life amongst algal foliage, high above the possibly turbid sediment/water interface. In other cases, unusual shell morphologies are readily interpreted as adaptations to life on a soft bottom. Thus, Peel (1975a) proposed that the widely expanded, explanate aperture of the Arisaig bellerophontacean *Anapetopsis* (Pl. 27, figs. 5, 6) was an adaptation to a soft bottom. A more generally significant example, the correlation between the high-spined shell form and low-energy environments (including infaunal) by Vermeij (1971), is more fully discussed below.

Determination of the former life habits of Lower Palaeozoic gastropods must depend heavily on the establishment of parallels between present-day and fossil morphological adaptations. Unfortunately, the average trochiform gastropod shell can be found in most present-day environments. In addition, widely different ranges of shell morphologies are present in Recent and Palaeozoic gastropod faunas as a result of evolutionary changes in faunal composition (Vermeij 1975). There are also dangers associated with such morphological comparisons, as can be readily seen from comparing the Recent pleurotomariids *Perotrochus*, *Mikadotrochus*, and *Entemnotrochus* with their very close morphological analogues from the Palaeozoic. The Recent species are restricted to deeper water, while the more abundant Palaeozoic species are demonstrably shallow-water dwellers. However, favourable parallels can often be established for more unusual morphologies. Thus, the soft-bottom mode of life inferred above for the explanate bellerophontacean *Anapetopsis* on morphological grounds, is supported by comparison with the present-day pelican's foot shells *Aporrhais pespelicani* and *A. serresiana* (Yonge 1937). Hyperstrophic, open coiling in the soft-bottom dwelling *Nevadaspira* from the Devonian led Yochelson (1971) to suggest a sedentary, ciliary feeding mode of life. Peel (1975d) suggested a similar existence for other Palaeozoic uncoiled and open-coiled gastropods, including forms resembling *Vermicularia*.

LIFE HABITS OF ARISAIG GASTROPODS

Different gastropod morphotypes in the Arisaig Group can be loosely assigned to three main life habits—soft-bottom dwellers, hard-bottom dwellers, and foliage dwellers—although some shell morphologies may occur in all three, e.g. high-spined gastropods. Assignment of individual morphological groups to trophic units is often unsatisfactory, since several groups contain gastropods that probably employed different methods of food gathering. Present-day high-spined gastropods, for example, may be ciliary feeders (*Turritella*), grazing herbivores, or deposit feeders (cerithiids), foliage dwellers (*Bittium*), or active infaunal predators (terebrids). However, all share certain common adaptive shell features which can be recognized in analogous Palaeozoic lineages. In this case, the possible feeding patterns of the Palaeozoic high-spined gastropods must then be deduced from evidence other than the basic shell morphology.

SOFT-BOTTOM DWELLING GASTROPODS

High-spined gastropods. High-spined murchisoniids and loxonematacean gastropods (Pl. 27, figs. 11, 14, 16, 19) are frequently abundant in assemblages from the Arisaig Group (text-fig. 2, species of *Murchisonia*, *Loxonema*, and *Morania*(?)). They form the dominant element in the soft-bottom, shallow marine platform fauna (text-figs. 5, 6), but may also be well represented in the hard-bottom, shallow marine platform fauna (text-fig. 4) and, to a lesser extent in the soft-bottom, open lagoon fauna.

The inability of the bipectinate ctenidia of Recent archaeogastropods to cope satisfactorily with fine, suspended sediment generally restricts members of the Order Archaeogastropoda to a firm bottom in conditions of clear water (Yonge 1947). Vermeij (1971) argued that the absence of the high-spined shell form amongst Recent archaeogastropods probably resulted from this restriction, since a high-spined shell is not physically stable in the higher-energy conditions associated with a hard bottom. The high-spined shell form is advantageous only in low-energy environments, or infaunally. The general equivalence of soft sediments and sea bottom with low-energy environments therefore tends to limit the high-spined shell form to the monopectinate caenogastropods, since archaeogastropod bipectinate ctenidia are unsuited to the turbid conditions in such an environment.

Loxonemataceans were considered to be caenogastropods by Knight *et al.* (1960) and, as such, probably moved freely in soft sediments. Murchisoniids, the most common Lower Palaeozoic high-spined gastropods, were only tentatively assigned to the Archaeogastropoda by Knight *et al.* (1960), since they combine the well-developed slit and selenizone characteristic of the Pleurotomariina and Bellerophontina with the high-spined form and other features of the Caenogastropoda.

Vermeij's (1971) stability arguments suggest that murchisoniids generally lived on a soft bottom in low-energy environments. Indeed, they may be common in fine sediments seemingly indicative of such conditions (Foerste 1923; Bretsky 1970). Consequently, murchisoniids are probably best interpreted as monopectinate caenogastropods, as also suggested by Bretsky (1970), although some form of modified bipectinate ctenidia unknown in extant archaeogastropods may have been present.

It must be remembered, however, that some Palaeozoic archaeogastropods, e.g. explanate bellerophontaceans, were apparently able to move freely over soft sediments. An alternative to the caenogastropod (or modified archaeogastropod) interpretation could be that murchisoniids were archaeogastropods with relatively normal bipectinate ctenidia, and that the post-Palaeozoic rise to dominance of caenogastropods with a more efficient monopectinate ctenidium may now effectively deny this environment to the less-efficient bipectinate archaeogastropods.

Some Lower Palaeozoic high-spired gastropods may have been ciliary feeders comparable to the present-day *Turritella* (Peel 1975*d*; 1977), scavengers, or even sluggish carnivores, on sedentary organisms in similar fashion to Recent epitoniids (Keen 1971; Morton and Miller 1973). However, most probably lived in a comparable way to extant herbivorous cerithiids. Many are microherbivores living on the algal-coated surfaces of fine sediments (Taylor 1971), as may have the murchisoniids and loxonematids dominating the soft-bottom, shallow marine platform fauna. Others live infaunally in sand (Keen 1971), which may partly explain the relatively large proportion of high-spired gastropods present in the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation (text-fig. 4). Other tiny species live amongst algal foliage (e.g. *Bittium*; Duffus 1969) and this mode of life can also be suggested for two small (less than 10 mm) Arisaig species—*Murchisonia s.l. antigonishensis* from the lower Moydart Formation, and *Morania*(?) sp. from the McAdam Brook Formation.

Explanate bellerophontaceans. Many unrelated bellerophontacean genera greatly increase the rate of whorl expansion in the final growth stage, so that the margins of the aperture become tangential to the substratum, i.e. explanate. Peel (1975*a*), in describing the explanate *Anapetopsis* (Pl. 27, figs. 5, 6) from the Stonehouse Formation at Arisaig, suggested that this morphology was an adaptation to life on a soft bottom. Enlargement of the gastropod foot associated with the expansion of the shell may have helped prevent submergence of the gastropod into soft sediment and could have lowered the amount of sediment raised into suspension by the gastropod's movements.

Phragmosphaera globata from the lower Moydart Formation is less bell-shaped than *Anapetopsis*, and has less finely tapering shell margins. It is possible that *P. globata* lived on a slightly harder bottom than *Anapetopsis*, by analogy with the present-day pelican's foot shell *Aporrhais*. The deeper water, soft-sediment dwelling *Ap. serresiana* has longer, more delicate digitations than occur in *Ap. pospelicani*, a thicker-shelled, muddy-sand dweller (Yonge 1937).

Explanate bellerophontaceans are characteristic of the soft-bottom, shallow marine platform fauna at Arisaig. *P. globata* is common in the lower Moydart Formation, while two species of *Anapetopsis* occur more rarely in the upper Stonehouse Formation (text-fig. 2).

A comparable relationship between explanate bellerophontaceans and a soft bottom has been described by Gromczakiewicz-Lomnicka (1972) from the Carboniferous of Poland. The bellerophontacean *Patellilabia*, a homeomorph of *Anapetopsis*, is the only large gastropod in a fauna of otherwise diminutive, algal-foliage dwelling gastropods in a black shale.

Trochiform murchisoniacean. The trochiform murchisoniacean *Seelya moydartensis* (Pl. 27, fig. 10) closely resembles members of the trochiform pleurotomariacean group characteristic of the hard-bottom, shallow marine platform fauna. However, the presence of an incipient anterior siphonal notch led Knight *et al.* (1960) to refer *Seelya* to the Murchisoniina, as a relative of the high-spired murchisoniids. The implied ability to move freely on soft sediment inherent in this systematic position, now that the Murchisoniina are considered to be caenogastropods or their functional equivalents, is substantiated by the Arisaig occurrence where *S. moydartensis* is associated with abundant high-spired gastropods and explanate bellerophontaceans in the soft-bottom, shallow marine platform fauna of the lower Moydart Formation.

Trochiform holopeids. *Gyronema haliburtoni* (Pl. 27, fig. 4) and *Holopea rossbrookiensis* (Pl. 27, fig. 1), the diagnostic element of the soft-bottom, open lagoon fauna are common in shales and mudstones in the lower part of the upper member of the Ross Brook Formation (text-fig. 2), which probably represent an originally soft bottom. The supposed bipectinate ctenidia of holopeids classically argues against life in such an environment, but this appears to be in conflict with the sedimentological evidence. It is possible that the holopeids were archaeogastropods adapted to soft sediment, or even that their affinities lie with the Caenogastropoda rather than with the Archaeogastropoda. Alternatively, holopeids may have lived amongst algal foliage in comparable fashion to members of a present-day trochid association in *Zostera* meadows noted by Morton and Miller (1973) in New Zealand. However, the Arisaig holopeids (up to 30 mm high) are relatively much larger than most of the trochids in the present-day association.

Trilobed plectonotinid bellerophontaceans are considered to be foliage dwellers, although their almost total absence (one recorded specimen) from the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation may indicate some correlation with a soft bottom. An alternative hypothesis involving a more off-shore origin for the Beechhill Cove Formation fauna than was suited to plectonotinids is discussed below.

HARD-BOTTOM-DWELLING GASTROPODS

The characteristic gastropods of the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation are trochiform pleurotomariaceans and certain trochiform platyceratids. A variety of other gastropods may also be present (text-figs. 2, 4) but are not considered to be diagnostic. Of particular note amongst these is the relative prominence of high-spired gastropods which characteristically dominate the soft-bottom, shallow marine platform fauna. The Beechhill Cove Formation high-spired gastropods are generally too poorly preserved for determination even to family, and therefore cannot be closely compared to forms in the rest of the Arisaig sequence. However, many probably lived infaunally, as do some recent cerithiids (Keen 1971), so that the low-stability shell (Vermeij 1971) was not exposed to the higher-energy environment at and above the surface of the sediment.

Trochiform pleurotomariaceans of the genera *Arjamannia* (Pl. 27, fig. 15), *Longstaffia* (Pl. 27, fig. 18), *Loxoplocus* (*Lophospira*) (Pl. 27, fig. 22), and *Phanerotrema* are common

in the Beechhill Cove Formation (text-figs. 1, 4) and form the diagnostic elements of the hard-bottom, shallow marine platform fauna. The rare Recent pleurotomariids *Entemnotrochus*, *Mikadotrochus*, and *Perotrochus* are morphologically very close to these extinct Palaeozoic genera, but are restricted to deep water (Batten 1958) in conditions quite unlike the shallow water, near-shore environment envisaged during the deposition of the Arisaig Group.

The presence of bipectinate ctenidia would be expected to limit trochiform pleurotomariaceans to a firm bottom in clear water (Yonge 1947), and this pattern is supported by their distribution at Arisaig. Many of the pleurotomariaceans reach a height in excess of 25 mm, suggesting life as epifaunal deposit feeders.

Trochiform platyceratids. The coprophagous habit of some platyceratids on echinoderms is well known (Bowsher 1955). Irregularities in the apertural margin of the gastropod (Pl. 27, fig. 2) commonly correspond to the shape of the surface of the echinoderm calyx. However, other platyceratids (e.g. *Cyclonema (C.) parvimum*, Beechhill Cove Formation; Pl. 27, fig. 23) have more regular growth lines and ornamentation and were probably benthic scavengers or sluggish carnivores on sedentary organisms. Large (20–30 mm) specimens of *C. (C.) parvimum* are typical of the hard-bottom, shallow marine platform fauna in the Beechhill Cove Formation. The genus is otherwise known at Arisaig only from a single poorly preserved specimen of *C. (C.) lydiamariarum* in the upper Stonehouse Formation (Peel 1975c).

ALGAL-FOLIAGE SUPPORTED GASTROPODS

In Recent assemblages abundant gastropods live among the foliage of marine algae and sea-grasses. The plants provide a protective habitat with abundant food above a possibly turbid sediment/water interface. Foliage-supported faunas are often well stratified, with distinctive suites of species living at the sediment surface, amongst the holdfasts or roots, and at various levels within the foliage (Morton and Miller 1973; Starmühlner 1969; Taylor and Lewis 1970). Stratification of faunas in algal foliage provides a possible explanation for the occurrence of archaeogastropods with ctenidia unsuited to turbid water in soft sediments, since undisturbed shell accumulations in such areas may include representatives from the pelagic realm, from any stratum within the foliage, from the sediment surface, or from the infauna.

The molluscs living on seaweed are generally small. Indeed, Brazier (1975) commented that an abundance of small gastropods may be one criterion for the recognition of former grass beds. Warmke and Almodovar (1963) studied the relationship between marine molluscs and algae in Puerto Rico and noted that gastropods comprised 99% of the molluscs in their samples. The vast majority of these were less than 2 mm in length.

Micromorphic gastropods are widely reported in the Palaeozoic (e.g. Gromczakiewicz-Lomnicka 1972; Harrison and Harrison 1975) but, especially in the Lower Palaeozoic, are often poorly preserved and systematically neglected. Most named and described Palaeozoic gastropods are significantly larger than most present-day foliage-supported species. Consequently, a general statement that many of these Palaeozoic gastropods were foliage dwellers is difficult to accept. Only one known

Arisaig gastropod species, *Tropidodiscus(?) arisaigensis* from the Doctors Brook Formation, falls within the 2-mm size parameter quoted by Warmke and Almodovar (1963), although this is undoubtedly a partial consequence of preservational and collecting bias.

Many smaller (c. 5 mm) Arisaig gastropods (e.g. *Cymbularia carinata*, *Naticopsis trevorpatriciorum*, *Murchisonia (s.l.) antigonishensis*, *Pharetrolites murchisoni* from the lower Moydart Formation) may also have been foliage dwellers, together with some gastropods reaching twice or three times this size. However, it is difficult to propose that a high proportion of Arisaig gastropods consistently attaining a size of 20 mm or more lived in this manner, although foliage support still provides an attractive interpretation of mode of life for a number of forms of this size discussed below.

The importance of size as a parameter distinct from morphology in evaluation of mode of life is clearly illustrated by comparing trochiform pleurotomariaceans from the Beechhill Cove Formation at Arisaig with their occurrence in the Carboniferous fauna described by Gromczakiewicz-Lomnicka (1972). The two groups of species are morphologically very close, but the epifaunal, deposit-feeding Arisaig specimens are commonly 20–25 mm high—some four or five times as large as the foliage-dwelling Carboniferous species. This size difference is paralleled within high-spined gastropods at Arisaig.

Micromorphic bellerophontacean. The minute, laterally compressed bellerophontacean *Tropidodiscus(?) arisaigensis* (length 2 mm), currently known at Arisaig only from the Doctors Brook Formation, was interpreted as a micromorphic adult by Peel (1977) and not as a juvenile of some otherwise unrecognized species. *T.(?) arisaigensis* is of comparable size to most Recent gastropods living amongst algal foliage (Warmke and Almodovar 1963; Morton and Miller 1973) and is one of the very few Arisaig species that can be interpreted confidently as having this mode of life.

Micromorphic high-spined gastropods. As noted above, *Murchisonia (s.l.) antigonishensis* from the lower Moydart Formation, and *Morania(?)* sp. from the McAdam Brook Formation may have lived amongst algal foliage in similar fashion to present-day cerithiids of the same size (Duffus 1969).

Trilobed bellerophontaceans. Peel (1974) discussed the functional morphology and systematics of the trilobed plectonotid bellerophontaceans *Plectonotus* and *Tritonophon* (Pl. 27, figs. 3, 8, 20) and concluded that trilobation increased the efficiency of the mantle cavity by separating the inhalant and exhalant respiratory currents. As a result of the generally accepted presence of bipectinate ctenidia, trilobed plectonotinids would be expected to favour a firm bottom in clear water, or to be foliage dwellers. The latter seems to be most likely since plectonotiniids, although often 10–15 mm in length, are commonly preserved in fine sediments probably indicative of a rather soft bottom. Bretsky (1970) suggested that a *Plectonotus(?)* sp. in the upper Ordovician of the central Appalachians browsed on algal fronds growing on the silty muds of extremely near-shore lagoons.

Plectonotinids appear to be associated with extreme near-shore conditions. Boucot *et al.* (1969) described a homalonotid-*Plectonotus* Community from the Silurian and Devonian to the landward of Ziegler's *Eocoelia* Community. Bretsky (1970) found

them to be characteristic of the most inshore, linguloid, population of his *Orthorhynchula-Ambonychia* Community. At Arisaig, plectonotinids are especially common in the soft-bottom, shallow marine platform faunas of the lower Moydart and upper Stonehouse formations, and in the shallow, shoaling deposits of Doctors Brook Formation. They occur more sparsely in the higher beds of the Ross Brook and McAdam Brook formations as a more near-shore equivalent of the trochiform, holopeid dominated soft-bottom, open-lagoon fauna. Plectonotinids are rare in the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation, where the abundance of *Bucanopsis* sp. may indicate slightly more off-shore conditions than were favourable to plectonotinids (see next section). Alternatively, their virtual absence from the Beechhill Cove Formation could reflect a preference for a softer bottom.

Other bellerophontaceans. A number of other small bellerophontaceans were probably grazers amongst algal foliage in similar fashion to trilobed plectonotinids. This foliage-supported mode of life is especially probable in the lower Moydart Formation, where *Pharetrolites purchisoni* and *Cymbularia carinata* are associated with abundant *Tritonophon trilobata* and other small gastropods (*Naticopsis trevorpatriciorum*, *Murchisonia s.l. antigonishensis*).

Bucanopsis sp. (Pl. 27, figs. 17, 21) is associated with trochiform holopeids in the shallowing cycles of the upper Ross Brook and McAdam Brook formations (text-fig. 2) prior to the incoming of trilobed plectonotinids. This separation of bellerophontaceans may suggest a preference by *Bucanopsis* sp. for slightly more off-shore conditions than those favoured by trilobed plectonotinids. The relative abundance of *Bucanopsis* sp. and the absence of plectonotinids in the Beechhill Cove Formation may suggest that the fauna of the latter lived under more off-shore conditions than the faunas of the lower Moydart and upper Stonehouse formations, where plectonotinids are common.

Lenticular pleurotomariaceans (*Liospira* cf. *L. affinis*, Beechhill Cove Formation; *L. marklandensis*, upper Stonehouse Formation, Pl. 27, figs. 7, 13; *Umbospira yochelsoni*, upper Ross Brook Formation, Pl. 27, fig. 9) have nearly planispiral shells, up to 25 mm in diameter, of similar morphology to laterally compressed bellerophontaceans. An epifaunal deposit-feeding, or foliage-browsing, mode of life is probable. Abundance of lenticular elements may be correlated with shallow water (e.g. compare the well-known *Turbocheilus* [*Platyschisma*] *helicites* beds associated with the transition from marine to non-marine strata in the Silurian of the Welsh Borderlands, the *Platyschisma* community of Boucot 1975). As such, they are abundant in both the hard-bottom, shallow marine platform fauna of the Beechhill Cove Formation and the soft-bottom, shallow marine platform fauna of the upper Stonehouse Formation. Their absence from the soft-bottom, shallow marine platform fauna of the lower Moydart Formation is unexplained, although a variety of small foliage-dwelling gastropods is present and may occupy that niche.

Other gastropods. Several small gastropod species are too rare at Arisaig to integrate into the above scheme, although a number were possibly foliage dwellers. This rarity may itself suggest that some of the species, e.g. the caenogastropod *Auriptygma* from the upper Stonehouse Formation, were carnivores (Boucot 1975), although supporting evidence is not available.

The two hyperstrophic species *Onychochilus(?) reversa* and *Mimospira abbae*, and the globose *Naticopsis trevorpatriciorum*, all between 5 and 10 mm high, were possibly foliage dwellers.

Three holopeid species (*Haplospira sibeluixeni*, an undetermined holopeid and an undetermined gyronematid) were probably members of the trochiform holopeid group discussed above. *Platyconus(?)* sp. and an undetermined trochonematid from the upper Stonehouse Formation, and an undetermined trochinid from the Beechhill Cove Formation, were probably epifaunal deposit feeders.

SUMMARY

Three basic types of gastropod fauna in the Arisaig Group of Nova Scotia are partially repeated in successive regressive phases of sedimentation (text-fig. 3). The morphological composition of the individual repeated faunas is largely unaltered, although taxonomic similarity between successive regressions is low (text-fig. 2).

A hard-bottom, shallow marine platform fauna is dominated by epifaunal, deposit-feeding trochiform pleurotomariaceans and benthic scavengers (*Cyclonema (C.) parvimum*). Infaunal, high-spined gastropods, and foliage-dwelling lenticular pleurotomariaceans and small bellerophonaceans (*Bucanopsis* sp.) are well represented.

A soft-bottom, shallow marine platform fauna is characterized by abundant epifaunal, deposit-feeding, high-spined murchisoniids and loxonemataceans. Associated elements include epifaunal deposit-feeding explanate bellerophonaceans and trochiform murchisoniaceans, and foliage-supported lenticular pleurotomariaceans, trilobed plectonotid bellerophonaceans, and other small gastropods.

A soft-bottom, open lagoon fauna is strongly dominated by deposit-feeding or foliage-dwelling trochiform holopeids, but these give way to small bellerophonaceans nearer shore.

Acknowledgements. R. K. Bambach, A. J. Boucot, and Rodney Watkins kindly supplied unpublished information. John M. Hurst and Eckart Håkansson criticized the manuscript, which is published by permission of the Director, Geological Survey of Greenland. A contribution to Project Ecostratigraphy.

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Original typescript received 4 February 1977

Revised typescript received 2 April 1977